SYSTEMATIC RELATIONSHIPS OF THE PEDICULOCHELIDAE (ACARI: ACARIFORMES)

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Abstract.—The enigmatic family Pediculochelidae has in the past been associated with two mite suborders, Prostigmata and Astigmata. Based on a cladistic analysis, we propose that the family represents a sister-group of the Haplochthoniidae and these mites thus should be considered highly derived members of the enarthronote "oribatid" mite superfamily Cosmochthonioidea. Similarities with other taxa of sarcoptiform mites and Astigmata are the result of symplesiomorphy or convergence. *Pediculochelus* Lavoipierre is considered a junior subjective synonym of *Paralycus* Womersley. The family Protoplophoridae is added to the superfamily Cosmochthonioidea; the genera *Nipponiella, Marshallia,* and *Trichthonius* are removed from the Cosmochthoniidae, but not reassigned pending further study. *Paralycus raulti* (Lavoipierre), *P. parvulus* (Price), and *P. lavoipierrei* (Price) are new combinations.

The statement by Price (1973) that mites constituting the monogeneric family Pediculochelidae "do not appear to be closely related to any known family of Acarina" seems to reflect the thoughts of the few acarologists who have studied the group. Thus, when Lavoipierre (1946) first proposed the family no affiliation with established mite suborders was suggested, except for reference to what can be considered superficial resemblance to members of the highly derived family Tarsonemidae (Prostigmata). Also indicative of their historically problematic position within accepted taxonomic frameworks is the opinion of Baker and Wharton (1952), who while including them in the Astigmata suggested that they represent an "intermediate form" between the latter group and "oribatid" mites. A number of subsequent workers (e.g., Dubinin, 1954; Yunker, 1955; Baker et al., 1958; Krantz, 1960) followed suit and included pediculochelid mites in the Astigmata as representatives of an isolated, primitive superfamily, the Pediculocheloidea. Apparently relying on different characters, Krantz (1970) voiced a modern consensus view that the closest relatives of these mites were to be found not among the Astigmata, but among the most primitive Acariformes, specifically the primitive Pachygnathoidea (= Endeostigmata sensu Grandjean, 1939); supportive discussion was not offered.

The present study, using previously unanalyzed characters and cladistic meth-

odology, will support our contention that the nearest extant relatives of Pediculochelidae are in neither of the above taxa, but rather the sarcoptiform mite group known as Enarthronota, specifically certain taxa in the superfamily Cosmochthonioidea. At first, such an association may seem unreasonable due to the absence in Pediculochelidae of a sclerotized integument, erectile notogastral setae, or other features often associated with cosmochthonioid mites. It will be demonstrated, however, that a number of derived (apomorphic) character-states of pediculochelid mites are shared only with this group, and most character-states suggestive of affinities with the Astigmata, Tarsonemidae, or "Endeostigmata" are ancestral (plesiomorphic) or represent convergences.

The Enarthronota is one of six major "oribatid" mite taxa recognized and defined by Grandjean (1969); his studies suggest that it is monophyletic. As noted elsewhere (Norton, 1982) it constitutes a number of seemingly isolated, relict families, most of which are poor in species. Considerable past evolutionary plasticity is disclosed by extant taxa, which exhibit a diversity of character states greater than that of any other major "oribatid" group except perhaps the species-rich Brachypylina. A ptychoid body form, for example, has evolved at least twice within the Enarthronota. It also contains some of the smallest known mites among the free-living Sarcoptiformes, and some with very regressive leg and palp setations.

Before specifically discussing the Pediculochelidae, we will review the status and relationships of the superfamily Cosmochthonioidea Grandjean, 1947. In this discussion we have hypothesized character state polarities using as outgroups several taxa (Pachygnathoidea, Terpnacaridae, Palaeosomata) which are considered to represent earlier derivative lineages in the Sarcoptiformes than that represented by the Enarthronota. Our concept of the superfamily Cosmochthonioidea is similar to that of Grandjean (1969) with the addition of the Protoplophoridae, which he treated as a distinct superfamily. Thus, at present it includes the families Cosmochthoniidae, Protoplophoridae, Sphaerochthoniidae and Haplochthoniidae. Recently, Balogh and Mahunka (1979), without discussion, have elevated the latter two taxa to superfamily rank and restricted the Cosmochthonioidea to the nominate family, thereby producing four monofamilial superfamilies. Although a certain amount of monotypy is expected in higher taxa with many relicts, we feel that their split classification is unjustified; relationships such as those proposed in this paper are masked by redundant categories (Wiley, 1979).

The following six synapomorphic character-states serve to define the Cosmochthonioidea (in the present sense) as a monophyletic group with a high level of confidence. Numbers 1 and 2 are autapomorphic, found in no other acariform mites; 3–6 are shared with a few groups outside the Enarthronota but are not found in earlier derivative enarthronote taxa, such as the Atopochthonioidea and Brachychthonioidea, or any other non-cosmochthonioid Enarthronota.

1. Pharyngeal cupola. The massive muscles which dilate the pharynx of cosmochthonioid mites originate on a thin, oval, plate-like and dorsally convex sclerite. This large internal sclerite occupies much of the proterosoma as seen in dorsoventral view and is easily seen by transparency in the Haplochthoniidae and Protoplophoridae, but may be difficult to observe without dissection in the more ornately sclerotized Cosmochthoniidae and Sphaerochthoniidae. Grandjean (1946b, 1948, 1954a) has illustrated and described this structure in the former

two families and called it the "coupole pharyngienne." It is an apodeme which forms as an internal extension of the dorsal wall of the subcapitulum where it meets the cheliceral frame; as such it appears to be derived from the small capitular apodeme of other sarcoptiform mites (Grandjean, 1954a, 1957a). Certain other arachnid groups have small apodemes in this location (cf. "epistomal apodeme" of Snodgrass, 1948). Inconspicuous, poorly developed homologues of this cupola are found in the Atopochthonioidea (Grandjean, 1948; Trave, 1967; Norton, 1982) and Hypochthonioidea (Grandjean, 1954a).

2. Pharyngeal sclerites. The large dilator muscles strongly taper anteroventrad and terminate in a pair of flat tendons which attach to a small discoidal sclerite on the dorsal wall of the pharynx at a level slightly posteriad of the true mouth opening. It is at this highly circumscribed location that the dilator muscles pull to expand the pharynx during the aspiration of food. Part of the ventral wall of the pharynx opposite this sclerite is also sclerotized and is fixed to the ventral integument of the subcapitulum by sclerotized bars or ligaments.

Such pharyngeal sclerites are unknown outside the Cosmochthonioidea. In sarcoptiform mites other than the Astigmata, the only sclerotized structures in this area are the inferior and superior (paired) commisural indurations (Grandjean, 1957b; Hammen, 1980) which are at the anterior extremity of the pharynx and support the mouth opening. The complex sclerotization of the pharyngeal region in some Astigmata (Akimov, 1979) represents an independent development quite unlike the structure described here. Also the dorsal dilator muscle bundles of other sarcoptiform mites are not similarly tapered and insert on the pharynx over a broad area. If tapered at all, they taper toward their origin on the dorsal wall of the subcapitulum or on a narrow capitular apodeme.

3. Setae of coxisternum II. Adults of all known Cosmochthonioidea have two pairs of setae on coxisternum II. The median pair is always larval and seems to be of sternal origin. The lateral pair is of coxal origin and appears in the proto-nymph (e.g., Cosmochthoniidae, Sphaerochthoniidae) or larva (Haplochthoni-idae). Polarity of this character is difficult to establish due to the differences in development of the coxal fields in the outgroups. A major problem is the pair of sternal setae which may be captured by either coxal fields I or coxal fields II in different outgroups, making simple numerical comparisons inaccurate. In the most distant outgroups examined, the earliest derivative Trombidiformes in the families Sphaerolichidae and Lordalychidae, adults bear two pairs of setae on the coxal areas of coxisterna II. Similarly, in the earliest derivative Sarcoptiformes, the Pachygnathidae and Nanorchestidae, adults bear at least two pairs in this region. This is also the case in some Palaeosomata and in the Alicorhagiidae, although in both groups the number of true coxal setae may be reduced to one pair in some taxa. The situation is complicated by the apparent loss of true coxal setae from coxisternum II in the Terpnacaridae and Oeserchestidae, other early derivative sarcoptiform taxa.

On the basis of these outgroups, it appears that the ancestral condition in the Sarcoptiformes is to have at least two setae on coxisternum II in the adult, indicating that the presence of this state in the Cosmoochthonioidea is primitive. However, when all other groups within the Enarthronota are examined, none are found to possess the lateral setae of coxisternum II at any stage of development. This synapomorphy suggests two hypotheses: either the Cosmochthonioidea is

the sister-group of all other Enarthronota, or the presence of true coxal setae on coxisternum II in the Cosmochthonioidea is the result of a reversal. On the basis of a number of other characters to be discussed elsewhere, we believe for the present time that the second hypothesis is more parsimonious. We suggest that this reversal is a synapomorphy which aids in the definition of the Cosmochthonioidea.

4. Posterior genital papillae. As tritonymphs and adults, all members of the Cosmochthonioidea have the most posterior of the ancestral three pairs of genital papillae regressive, either reduced in size or lost altogether (*Amnemochthonius, Cryptoplophora*). All papillae are relatively large in non-cosmochthonioid Enarthronota. Similar trends in the Astigmata and in a few isolated Palaeosomata and Brachypylina are regarded as convergences.

5. Genual solenidia of adult. Cosmochthonioid mites exhibit the highest degree of solenidial regression known in sarcoptiform mites, outside of the very primitive but highly aberrant Nanorchestidae. In particular they have lost the genual solenidia (σ) on all legs and in all instars. They are the only sarcoptiform mites outside the Nanorchestidae which have completely lost σ on genu I (Grandjean, 1964)[1]. Similarly, only the Pterochthoniidae and a few Astigmata share the loss of σ on genu II and only the former, plus a few Nothroidea (Desmonomata), the genus *Micreremus* (Brachypylina) and numerous taxa in the Astigmata share the loss of σ on genu III. All Brachypylina (except *Liodes*), many Nothroidea and Phthiracaroidea (sensu latu), and all Astigmata share the loss of σ on genu IV, but among the Enarthronota and its close outgroups only the Pterochthoniidae exhibit this synapomorphy.

6. Fusion of palpal segments. The palp of cosmochthonioid mites exhibits a tendency to lose the movement between femur and genu. In most of the included taxa, the two segments are separated by a complete suture, but the joint lacks articulating membrane and thus its function. In some genera (*Amnemochthonius, Cryptoplophora*) the dividing suture may be partially effaced. Such a fusion is found in isolated instances in more highly derived sarcoptiform mites, but not elsewhere within the Enarthronota.

INCLUSION OF THE PEDICULOCHELIDAE IN THE COSMOCHTHONIOIDEA

Based in part on the descriptions of Price (1973), but mostly on the study of adult specimens of *Pediculochelus lavoipierrei* Price from California, a related species from Western Australia, and a few adult *P. parvulus* Price, it can be concluded that all six of the synapomorphies discussed above as defining the superfamily Cosmochthonioidea are shared by the Pediculochelidae.

The complex pharyngeal aspiratory apparatus of the Pediculochelidae is quite distinct. The pharyngeal cupola is broad in dorsal aspect although somewhat less strongly convex than in the other cosmochthonioid families. In Fig. 3 its lateral contour is indicated by *vpx*. The pharyngeal sclerites are distinct, especially since

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[1] It appears that Grandjean (1950) overlooked a small solenidial vestige on genu I of *Pterochthonius angelus* (Berlese) which is discernible only in dorsal aspect. All North American specimens we have examined possess this vestige.

they are the most heavily sclerotized parts of the body and the only ones with a brownish coloration. The dorsal disk (*dk*) is small and somewhat oblong; the bases of the tendons are apparent, but the dilator muscles which insert here and originate on the cupola have been destroyed by clearing in all specimens observed. The ventral sclerite (*vs*) and supportive ligaments are much more conspicuous than the disk.

Coxisternum II has two pairs of setae in the adult instar. In *P. lavoipierrei* (but not other described species) the medial pair (which appears to be of sternal origin) is several times the length of the lateral pair. When the second seta appears is not known, but it is absent on the single larval specimen we studied.

The genital papillae of pediculochelid mites are distinctly regressive, both in number and stature. All described species have only two pairs in the adult (it is presumably the posterior pair which is lost) and they are small, disc-like structures. It is also interesting that Grandjean's (1946b, 1948) concept of homeotypy of genital papillae and Claparede's organ of the larva is supported by their states in *P. lavoipierrei*; corresponding to a reduction in size and number of genital papillae of nymphs and adult, Claparede's organ (urstigma) is absent in the larva. Outside the Astigmata, this is the only sarcoptiform mite known where such a loss is complete; a very reduced organ is found in the larva of *Haplochthonius* and Grandjean (1948) hypothesized its loss in *Amnemochthonius,* whose larva is unknown.

The leg solenidial formula (genu to tarsus, legs I–IV) of *P. lavoipierrei* is (0-1-1) (0-0-1) (0-1-0) (0-0-0). It is unlikely that it differs in other species, since intrageneric variation in these characters is unknown elsewhere in the Enarthronota and even intrafamilial variation is rare. All genual solenidia are lost, as in other Cosmochthonioidea, and further losses make this the second most regressive formula yet known in sarcoptiform mites, with only that of *Speleorchestes* (Nanorchestidae) being more regressive.

The palp of pediculochelid mites is similar to that of other cosmochthonioid mites in having a non-functional femur-genu articulation. There is no membrane associated with the joint and the suture is effaced paraxially.

RELATIONSHIPS WITHIN THE COSMOCHTHONIOIDEA

To aid in further substantiating the placement of the Pediculochelidae in the Cosmochthonioidea, a preliminary cladogram will be offered as a hypothesis of phylogeny within the group. A more detailed study of enarthronote phylogeny is in progress and will deal with other characters, including those showing a greater amount of homoplasy, and a reclassification will be proposed. In this section character-state polarities have been hypothesized using as outgroups those mentioned previously and all non-cosmochthonioid Enarthronota. Characters 7–18 are discussed below and support our hypothesis that the Pediculochelidae are most closely related to the Haplochthoniidae. Whether or not the two families can be considered sister groups, or more precisely, whether or not the Haplochthoniidae is monophyletic with respect to the Pediculochelidae, will be addressed in the next section.

7. Scissure ar_1. Grandjean (1946b) used this designation for the band of unsclerotized integument separating the dorsal plates bearing setal rows *c* and *d* of enarthronote mites. From outgroup comparison, this scissure was ancestrally (with

respect to the Cosmochthonioidea) what Grandjean called a "type E" scissure, a simple narrowed, unspecialized band of flexible cuticle. There are some reasons, which will not be addressed here, to believe that this scissure is derived from a "type S" scissure (where a row of erectile notogastral setae is inserted on intercalary sclerites) in which the intercalary sclerites fused to the plate posterior to it. The "type E" scissure, however it originated, is found in the Cosmochthoniidae and Haplochthoniidae. Sphaerochthoniidae and Protoplophoridae possess a further derived "type L" scissure, in which the anterior plate developed a large tectum partially overlapping the posterior plate. There is a relatively broad expanse of flexible cuticle between the plates which is hidden beneath the tectum and provides a telescoping dorsal articulation between the two secondarily formed parts of the notogaster (pronotaspis and pygidium). The character does not exist in pediculochelid mites, which lack sclerotized hysterosomal integument, but there is a definite constriction and a break in cuticular striation between setal rows c and d.

8. Setal row d. Concomitant with the development of a tectum overhanging scissure ar_1, setae d_1 and d_2 of the Sphaerochthoniidae and early derivative Protoplophoridae have become regressive; they are minute and inserted near the anterior margin of the pygidium. In *Cryptoplophora* these setae have been completely lost in the adult instar, but remain as vestiges in the immatures (Grandjean, 1954a). In other Cosmochthonioidea, and all other Acariformes in which "notogastral" setae are present and homologies can be ascertained, setae d_1 and d_2 are exposed and comparable in stature to those of row c. The Atopochthoniidae (Enarthronota) is the only possible exception; Grandjean (1948) suggested that setal row d was lost in this monotypic family.

9. Scissures ar_2 and ar_3. Outgroup comparisons suggest that these scissures were ancestrally "type S" scissures with large erectile setae. In the Sphaerochthoniidae and Protoplophoridae fusion of the anterior, posterior and intercalary plates associated with the respective scissures has taken place in the adult instar, leaving a raised, transverse carina (state 9a); a simple scissure with no intercalary sclerite is present in immatures. In the Cosmochthoniidae the ancestral condition is retained. We feel the sclerotized adults of haplochthoniid mites have derived secondary type E scissures at ar_2 and ar_3 by the complete fusion of the intercalary sclerites with the respective plate posteriad of them (state 9b). Grandjean (1946b) has illustrated notches in the plates which cause the setae to, in effect, border the unsclerotized integument of the scissures. The Pediculochelidae and the unsclerotized immatures of Haplochthoniidae do not possess these characters. Members of the former family do show constrictions and loss of integumental striations midway between setal rows e–f and f–h, as illustrated by Price (1973) (his rows d–e and e–f, respectively), but we believe such constrictions are secondarily derived. Many mites which have evolved an elongated body form also develop secondary constrictions or articulations which allow bending of the hysterosoma (e.g., many Prostigmata, the Mesostigmata family Rhodacaridae and the sarcoptiform mite families Elliptochthoniidae and Gehypochthoniidae).

10. Setal rows e and f. Outgroup comparisons with the Palaeosomata and other Enarthronota suggest that these setae were ancestrally large and erectile in the Cosmochthonioidea and associated with the type S scissures noted above. They

retain this state only in the Cosmochthoniidae. Erectility has been lost in the other families due to fusion of intercalary sclerites as noted in character 9. The setae may be similar in size and shape to other notogastral setae (Sphaerochthoniidae, Haplochthoniidae, Pediculochelidae) or retain a somewhat larger size (Protoplophoridae).

11. Solenidion ω_2 of tarsus I. When present, this solenidion is formed in the protonymph except in the genus *Hermannia* (Desmonomata), where its appearance is delayed. Ancestrally in sarcoptiform mites, and in all Enarthronota except the Cosmochthonioidea and Brachychthonioidea, ω_2I is present and positioned on the dorso-antiaxial surface of the tarsus (Grandjean, 1963). In the Sphaerochthoniidae and Protoplophoridae ω_2I has moved to a ventral location and is closely coupled to a normal seta, m'' (state 11a), except in *Cryptoplophora* where m'' has been secondarily lost. Among other Enarthronota only the Brachychthoniidae have a ventral ω_2I; in these mites it is closely coupled with ω_3I rather than m'', which is absent. The latter family is only distantly related to cosmochthonioid mites and we consider this positional similarity a convergence. The Cosmochthoniidae, Haplochthoniidae and Pediculochelidae have lost ω_2I, a regressive state (11b) found elsewhere in sarcoptiform mites only in the genus *Camisia* (Desmonomata) and some groups in the Astigmata. We feel the ancestral condition in sarcoptiform mites noted above is also ancestral in the Cosmochthonioidea; the two apomorphic states exhibited by extant taxa have been derived independently, rather than state 11a giving rise to state 11b after ω_2I had moved ventrad. The latter alternative would require the loss of the solenidion after coupling with m'' and also the retention of m'' (Cosmochthoniidae and *Haplochthonius* retain this setae, *Amnemochthonius* and Pediculochelidae have lost it). However, throughout sarcoptiform mites the tendency is the reverse, that is, for the normal seta to be lost (ontogenetically or phylogenetically) after coupling rather than the solenidion; we know of only one example (discussed below) where the solenidion of such an association regresses, leaving the seta alone.

12. Solenidion ω_3 of tarsus I. This solenidion is present in all tested outgroups, notably the non-cosmochthonioid Enarthronota, except the Hypochthonioidea and *Heterochthonius*: we consider it ancestrally present in the Cosmochthonioidea. The Sphaerochthoniidae and Protoplophoridae have retained it, but it is lost in the Cosmochthoniidae, Haplochthoniidae and Pediculochelidae.

13. Anterior and middle genital papillae. These papillae are highly reduced in the Cosmochthoniidae, Pediculochelidae, and Haplochthoniidae except for *Amnemochthonius,* which has lost them altogether. The Sphaerochthoniidae and Protoplophoridae retain the ancestral condition of having normal, large anterior and middle papillae.

14. Genital vestibule. As adults, members of the Cosmochthoniidae and Haplochthoniidae have developed very large, elongated genital plates which cover a genital vestibule, or pregenital chamber, which is several times larger than necessary for containment of the small external genitalia. The vestibule is equally enlarged in the Pediculochelidae, but the integument forming the external valves is not sclerotized. Sphaerochthoniidae and Protoplophoridae retain the ancestral condition of having genital plates and a genital vestibule of normal proportions.

15. Genital tracheae. Adults of the Cosmochthoniidae and the genus *Haplochthonius* possess two distinct pairs of tracheae, with bulbous terminations,

which open into the large genital vestibule at its anterior and posterior limits, respectively. The other known haplochthoniid genus (*Amnemochthonius*) has only the anterior pair, which in the former taxa are always the larger of the two and the first to form in ontogeny. The Pediculochelidae have no genital tracheae, but there is a pair of distinct angular cavities (Fig. 4, *trv*) with a position exactly corresponding to the openings of the anterior tracheae of the above taxa; we believe these are vestiges of the anterior pair. Tracheae opening into the genital vestibule are unknown in other "oribatid" mites (including Sphaerochthoniidae and Protoplophoridae) but have evolved independently in certain other Acariformes (e.g., Bdelloidea, Sphaerolichidae, some Nanorchestidae and some Astigmata).

16. Sclerotization of immature hysterosomal integument. It is usual in the Enarthronota (and here considered ancestral) for the immature instars to have a hysterosomal integument which is at least partially sclerotized dorsally and ventrally; lateral sclerotization may be present or absent. This ancestral condition is found in the immatures of the Sphaerochthoniidae, Protoplophoridae and Cosmochthoniidae. Members of the Haplochthoniidae and Pediculochelidae have completely lost this sclerotization and, as immatures, possess a soft, striated integument over the whole hysterosoma. Members of most other sarcoptiform groups also have immatures with unsclerotized hysterosomal integument, but it normally lacks fine striations. Grandjean (1948) considered all soft striated integument to be "primitive" integument, that is, not a result of secondary desclerotization. Outgroup comparisons with other Enarthronota do not support that conclusion within the Cosmochthonioidea, suggesting the hypothesis that such desclerotization has in fact occurred in the Haplochthoniidae and Pediculochelidae.

17. Rostrum. Stegasimy, the presence of sclerotized rostrum with a well defined tectum, is widespread in the Enarthronota and its presence in both adults and immatures is probably ancestral in the Cosmochthonioidea. In the Sphaerochthoniidae and Protoplophoridae the rostral tectum is similar in ornamentation to the rest of the prodorsum, as it is in non-cosmochthonioid Enarthronota which possess this character state. Members of Cosmochthoniidae have developed a curious fenestrate rostral tectum (state 17a) which has been described by Grandjean (1962). The adults of *Haplochthonius* have the ancestral state, but the immatures of this genus, and all instars of *Amnemochthonius* and the Pediculochelidae, have lost the rostral sclerotization (state 17b), thereby becoming secondarily astegasime (mouthparts not covered by a rostral tectum).

18. Solenidion ϕ of tibia IV. Outgroup comparison suggests that this solenidion was ancestrally present in the Cosmochthonioidea. It is retained by the Sphaerochthoniidae, Protoplophoridae and Cosmochthoniidae but is lost in the Haplochthoniidae and Pediculochelidae. It was also lost, apparently independently, by three other enarthronote taxa (the Hypochthonioidea, Mesoplophoroidea and Heterochthoniidae) and a number of more highly derived sarcoptiform groups (Grandjean, 1964).

The distribution of the character states discussed above (7–18) and summarized in Fig. 1 suggests an early division of cosmochthonioid stock (lineage I) into two principal lineages. Lineage II represents an unnamed taxon defined by three progressive synapomorphies (type L scissure ar_1, fused cariniform scissures ar_2 and
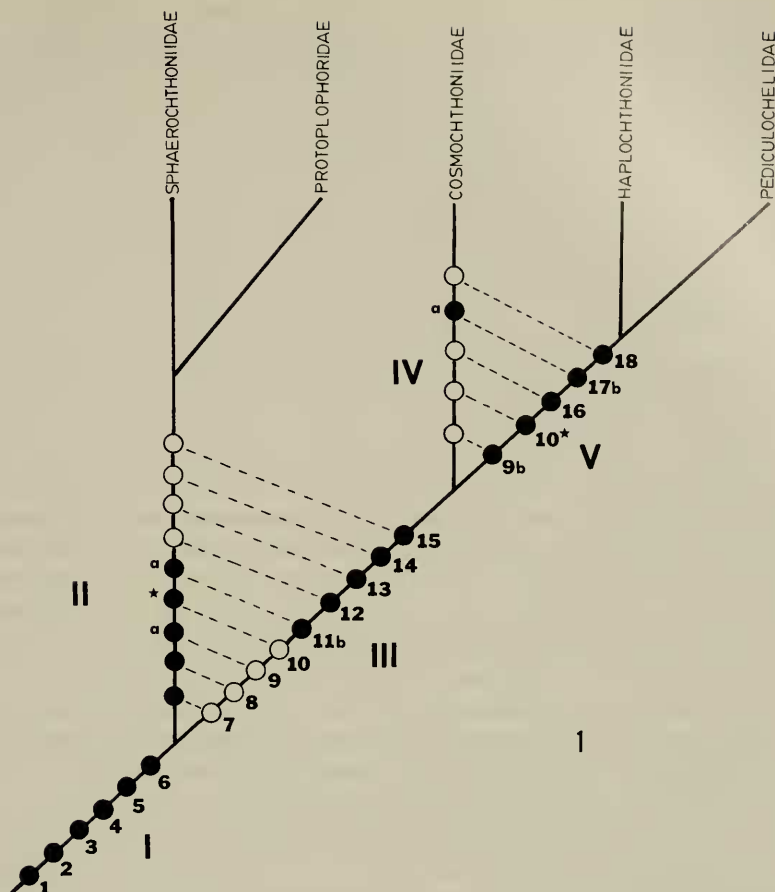
Fig. 1. Cladogram suggesting relationships of families in the Cosmochthonioidea. Numbers correspond to characters discussed in text; apomorphic states represented by ●, plesiomorphic states by ○; letters indicate different apomorphic states of same character; stars indicate convergent development of same apomorphy.

ar_3, and solenidion ω_2I coupled with ventral seta m'') and one regressive synapomorphy (size diminution or loss of opisthosomal setal row d); all are autapomorphic at this level. For the purposes of the present study there is no need to establish the monophyly of the Sphaerochthoniidae and Protoplophoridae. The latter have the conspicuous ptychoid body form, but Grandjean (1954a) has noted variety in the details of its sclerotization patterns. Ontogenetic studies of both families are needed and a detailed redescription of some member of *Hauseroplophora,* which are ptychoid mites with an otherwise sphaerochthoniid facies, would be useful.

Lineage III represents an unnamed taxon defined by two progressive synapomorphies (enlarged genital vestibule, presence of two pairs of genital tracheae) and three regressive synapomorphies (size diminution of anterior and middle genital papillae, loss of solenidia ω_2I and ω_3I); the former two are autapomorphies.
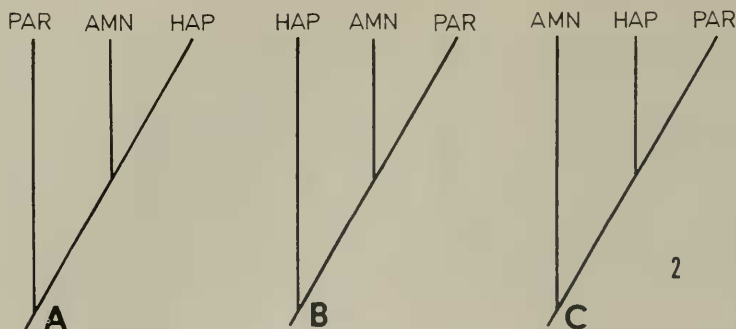
Fig. 2. Possible cladistic relationships of *Paralycus* (PAR), *Haplochthonius* (HAP), and *Amnemochthonius* (AMN). See text for explanation.

Lineage IV represents the Cosmochthoniidae with three nominate genera, *Cosmochthonius, Phyllozetes*, and *Krivolutskiella*. It retains numerous ancestral states but can be tentatively defined by one progressive synapomorphy (the fenestrate rostrum), which is autapomorphic. Genera previously included in the Cosmochthoniidae (Gordeeva, 1980), but removed by us are *Marshallia, Nipponiella* and *Trichthonius*; they share none of the synapomorphies discussed to this point. Placement of these taxa will be suggested in a subsequent paper.

Lineage V represents an unnamed taxon which includes the Haplochthoniidae and Pediculochelidae. It can be defined by three regressive synapomorphies (secondary development of astegasimy in immatures, loss of sclerotization of hysterosomal integument and the loss of solenidion ϕ IV) and one progressive synapomorphy (the partial fusion of intercalary sclerites at ar^2 and ar^3). It could be argued that integumental desclerotization as a whole should be treated as one character state, but hysterosomal and rostral sclerotization do not always occur together (Norton and Metz, 1980; Norton, 1982). There are also numerous losses of leg setae in lineage V; these will be analyzed elsewhere.

RELATIONSHIPS OF THE PEDICULOCHELIDAE AND
HAPLOCHTHONIIDAE

Assuming monophyly of lineage V, the remaining question in this analysis is whether the Haplochthoniidae and Pediculochelidae can be considered sister groups, or whether the Pediculochelidae originated within the Haplochthoniidae. Three genera are involved; *Haplochthonius* and *Amnemochthonius* constitute the Haplochthoniidae; *Paralycus* (see remark #1) represents the monogeneric Pediculochelidae. Three competing hypotheses, indicated by different cladograms (A, B, C) are illustrated in Fig. 2. Cladogram A assumes that the Haplochthoniidae is monophyletic; B and C assume paraphyly in this family, with *Paralycus* more closely related to *Amnemochthonius* (B) or *Haplochthonius* (C).

To aid in choosing the most congruent hypothesis, we have analyzed 48 characters found to be shared by two of the three taxa. Cladogram A is supported by five synapomorphies shared by members of *Haplochthonius* and *Amnemochthonius*, but not *Paralycus*. Three of these states are considered results of progressive

evolution: a) there is a medial paired row of five additional notogastral cupules located adjacent to the bases of setae c_1 to h_1, a condition otherwise unknown in the Acariformes; b) the labrum has become very thick, short and blunt, as opposed to the thin, tapered or pointed labrum found in *Paralycus* and other enarthronote taxa; c) the famulus is greatly enlarged relative to the size of tarsus I and has a hollow "root" projecting into the segment, a state unknown in other enarthronote mites. Two of the synapomorphies are considered results of regressive evolution: a) loss (or variable presence) of coxisternum III seta *3c,* a loss found elsewhere in sarcoptiform mites only in the Astigmata and a few Brachypylina and Desmonomata; b) loss of tarsal seta *ft′* on leg II, a seta retained by *Paralycus.* In addition, the general facies of *Haplochthonius* and *Amnemochthonius* are very similar and differ considerably from that of *Paralycus.*

Cladogram B is supported by 42 synapomorphies shared by *Amnemochtonius* and *Paralycus,* but not *Haplochthonius.* All are considered regressive and include: a) loss of the five pairs of ancestral cupules (*ia, im, ip, ih, ips*) in the adult instar; b) loss of Claparede's organ in the larva (presumed in *Amnemochthonius*); c) loss of the posterior pair of genital papillae in nymphs and adult; d) loss of the posterior genital trachea from deutonymph through adult; e) loss of adult rostral sclerotization leading to secondary astegasimy; f) loss of three pairs of genital setae in the adult (four pairs, compared to seven in *Haplochthonius*); g) loss of adanal seta ad_4; h) loss of anal seta an_4; i) loss of coxisternum IV seta *4d*; j) the loss of 27 leg setae (present ancestrally in the adult instar in lineage V) from femur I (*l′, l″*), tarsus I (*m″, it′, it″, pv′*), trochanter II (*v′*), femur II (*l′, l″*), genu II (*v*), tarsus II (*it″, a′, a″, pv′*), trochanter III (*l′*), femur III (*l″*), genu III (*l″*), tibia III (*l′*), tarsus III (*a′, a″, pv′*), trochanter IV (*v′*), genu IV (*l″*), tibia IV (*l′*) and tarsus IV (*a′, a″, ft′*). Character states included in a, b, c and many in j are found only in these two genera, except for some parallel setal losses in the Astigmata.

Cladogram C is supported by a single regressive synapomorphy shared by *Haplochthonius* and *Paralycus*: the loss of seta *l″* on tibia I. The hypothesis it represents can be quickly rejected as being least congruent with the distribution of synapomorphies.

Based only on minimization of homoplasy, cladogram B is most congruent and is supported by seven times as many synapomorphies as cladogram A. However, the fact that all 42 are regressive, and 33 of these are setal losses, detracts somewhat from the influence of these numbers. Grandjean's studies (e.g., 1946a) are replete with information on priorities in setal regression and it is clear that losses usually occur in identical sequences even in different lineages of a major group. Since setal regression has been so widespread in the evolution of sarcoptiform mites, we can expect, and indeed find, that homoplasy is extremely common when dealing with presence or absence of body and leg setae, either in the form of parallelism or, less commonly, convergence. Genital papillae and Claparede's organ also show regressive trends in the Cosmochthonioidea, and it should not be surprising to find parallel continuation of these trends in two different, but closely related lineages. Regressive trends toward secondary astegasimy, loss of posterior genital tracheae, and loss of normal cupules also appear well established in lineage V, since some or all immature instars of *Haplochthonius* exhibit them to some degree; these also might be expected to continue independently in different lineages.

On the other hand, the three unusual progressive states supporting cladogram A are difficult to explain in terms of parallelism or convergence. Nowhere else in the Enarthronota do we find medial cupules, a short, thick labrum or an enlarged "rooted" famulus. It is our contention that cladogram A is least easily rejected despite the relatively large amount of homoplasy it requires.

The simplest explanation for a majority of the synapomorphies shared by *Amnemochthonius* and *Paralycus* is one of neoteny; states ancestrally exhibited by immatures in lineage V are now exhibited by adults of these genera, through the delay or eventual loss of ontogenetic changes. Considering the losses listed above, members of the genera *Amnemochthonius* and *Paralycus* are among the most regressive sarcoptiform mites known, and this is probably a result of the greatest accumulation of neotenic character states. Interestingly, many of the same losses are characteristic of the Astigmata, a later sarcoptiform lineage which exhibits even more extreme neoteny (OConnor, 1981).

Not all setal losses can be thought of in this way, however. For example, the eugenital setae are not found in immature instars, yet are subject to numerical regression in adult mites. The Pediculochelidae have only two pairs of minute eugenital setae (Fig. 4, *eg*) inserted on the walls of the genital vestibule (there is no ovipositor); this is the lowest number known in sarcoptiform mites outside the Astigmata, which lack eugenital setae altogether.

REJECTION OF PREVIOUSLY SUGGESTED RELATIONSHIPS

Price (1973) has summarized the similarities of Pediculochelidae with members of other mite groups. Similarities with the Astigmata include: a) the absence of stigmata and associated tracheae; b) the unsclerotized integument; c) the padlike structure of the ambulacrum. The first is partly the result of symplesiomorphy, partly convergence. The prodorsal stigmata found in most Trombidiformes (= Prostigmata) are restricted to that suborder, and early derivative sarcoptiform mites such as the Enarthronota never possessed the acetabular stigmata found in the Brachypylina, a more highly derived group. There is strong evidence (OConnor, 1981) that the Astigmata were derived from a sarcoptiform mite lineage which did not possess these latter stigmata, so that from one standpoint their absence in the two taxa in question is symplesiomorphic and not useful in determining relationships. The Pediculochelidae have lost the genital tracheae which were once present, however, and from this standpoint the similarity is a result of convergence. Unsclerotized integument in both immatures and adults is a regressive state derived independently in the two taxa. The padlike ambulacrum of pediculochelid mites is, in detail, unlike any found in the Astigmata and cannot be considered a synapomorphy (see remark #2).

Although previous workers have not noted the details, a number of losses of leg setae represent similarities between the Pediculochelidae and Astigmata. Compared with earlier derivative sarcoptiform groups, both of these taxa share the loss of a considerable number of homologous setae. However, these losses are far from being in total agreement. The Pediculochelidae, for example, lack the following setae ancestrally retained in the Astigmata (setal homologies for the Astigmata following OConnor, 1981): genu III (*l'*); tibiae I–II (*v''*); tarsus I (*pl''*, *a'*, *pv'*, *pv''*, *tc'*, *tc''*). Conversely, all Astigmata lack the following setae retained

in the Pediculochelidae: femora I–IV (d); femur III (ev'); genu I (d); tibia I (l'); tibia II (d, l', l''); tibiae III–IV (d); tarsus I (a''). The number of non-homologous setal losses in these two groups suggests convergence in the setal regressions shared between them, especially as the lost setae are also commonly regressive in other groups (see above).

Similarities with the "Endeostigmata" noted by Price reflect the paraphyletic nature of that taxon. The "Endeostigmata" has traditionally been considered as part of the suborder Trombidiformes (= *Prostigmata*). OConnor (1981) has analyzed the phylogenetic position of each of the included taxa and hypothesized that most of the families usually included represent the earliest radiations of the Sarcoptiformes, with only two, the Sphaerolichidae and Lordalychidae actually belonging to the Trombidiformes in a phylogenetic sense. Using these hypotheses, it is apparent that most of the character states mentioned by Price as shared between the Pediculochelidae and the "Endeostigmata" represent symplesiomorphies. These ancestral states include a) the presence of prodorsal trichobothria; b) the presence of rutella; c) chelate "mouthparts"; d) simple palps; e) genital papillae. Of the other three character states listed by Price, one, small size, is found in so many different acarine lineages as to be of little value in phylogeny reconstruction. A second, the "segmented" appearance of the body, is ancestral in some "Endeostigmata," notably the Pachygnathidae, but is probably secondarily derived in the Pediculochelidae as noted earlier. Finally, the absence of sclerotized plates is again ancestral in the "Endeostigmata" but apparently secondarily derived through neoteny in the Pediculochelidae.

Similarities with Tarsonemidae (Trombidiformes) noted by Lavoipierre (1946) include segmented appearance and a large (clavate) sensillus. Whether or not the "segmentation" exhibited by pediculochelid mites is derived, it still differs from the pattern found in the Tarsonemidae and neither can be ancestral to the other. Of the three principal dorsal divisions, the Pediculochelidae have the middle one between setal rows e and f, whereas tarsonemid mites and their close outgroups have these rows on the same plate, the middle division being between rows d and e (Lindquist, 1977). The various "segments" of the dorsal hysterosoma are therefore not homologous. A clavate form of sensillus has been independently derived a great number of times in acariform mites (including in the Haplochthoniidae) and thus is not, by itself, a reliable indicator of relationships. More significantly, Lindquist (1976) has presented carefully conceived hypotheses on the phylogeny of the Heterostigmata (of which the Tarsonemidae is a part) and its outgroups. Except for a few convergent character states, such as the loss of Claparede's organ (urstigma), the fusion of the palpal femur and genu, and some superficial similarities in the ambulacrum, the Pediculochelidae do not share the synapomorphies of these taxa.

Despite the dissimilarity in facies between the Pediculochelidae and most cosmochthonioid mites, there is substantial accumulation of progressive synapomorphies as we pass from lineage I to III to V in Fig. 1. Especially significant are the autapomorphies associated with the pharyngeal aspiratory apparatus (cupola, musculature and pharyngeal sclerites) and the genital region (vestibule, tracheae). As just noted, the similarities between this family and the Astigmata, "Endeostigmata" and Tarsonemidae can be more easily dismissed as symplesiomorphies, common convergences or misinterpretation of homologies.

REMARKS

1. Price (1973) has commented on the possible synonymy of the generic name *Pediculochelus* Lavoipierre with *Paralycus* Womersley. He correctly suggested such a synonymy should be reserved until after a reinvestigation of the type specimen of *Alicus* (sic) *pyrigerus* Berlese, which Womersley (1944) designated as type-species of *Paralycus*. One of us (DEJ) has studied this specimen, housed in the Berlese Collection of the Stazione de Entomologia Agraria, Florence, Italy, and the subjective synonymy, first noted by Johnston (1965), is formally proposed here. The nominal species of *Paralycus* now include: *Paralycus pyrigerus* (Berlese), from soil in Italy; *Paralycus raulti* (Lavoipierre) **n. comb.**, collected with bees in South Africa; *Paralycus parvulus* (Price) **n. comb.**, from soil in California; and *Paralycus lavoipierrei* (Price) **n. comb.**, also from soil in California.

2. The small size of the ambulacrum of *Paralycus lavoipierrei* makes interpretation and illustration of minute detail very difficult, but the basic structure is illustrated in Figs. 5 and 6. The distal part of the tarsus forms a long stalk, similar to that of many other cosmochthonioid mites, except that the dorsal half is unsclerotized for almost the whole length of the stalk. The proral setae (p) are inserted approximately at the level where the dorsal integument becomes sclerotized. The distal pad has thin, rounded "wing-like" lobes projecting ventrodistad, so that it appears heart-shaped in dorsoventral aspect. The modified empodial claw (hatched in Figs. 5 and 6) provides a thick central support; it is nowhere freely projecting and its distal end blends indiscernibly with the pad rather than ending in a point. The dorsal unsclerotized integument of the tarsal stalk is continuous with that of the pad. Unlike the ambulacrum of the Astigmata (Grandjean, 1943; Atyeo, 1979), there are no condylophores. The latter are absent in all Enarthronota but usually present in more highly derived sarcoptiform mites, including the Astigmata. Whereas the general form of the ambulacrum of the Astigmata suggests that the unsclerotized distal end of the tarsus has become hypertrophied and envelopes the empodial claw (when present), that of *Paralycus* may be a result of winglike outgrowths from the epiostracum of the empodial claw itself.

3. The following are lists of body setae found on adults of *P. lavoipierrei* homologized with those of the system developed for "oribatid" mites in the various studies of Grandjean. Following each in parentheses is the letter-number designation given by Price (1973). Prodorsum: *ro* (v), *le* (p-2), *exa* (p-3), *exp* (p-4), *in* (p-5). Hysterosomal dorsum: c_1 (a-1), c_2 (a-2), c_3 (b-2), *cp* (b-1), d_1 (c-1), d_2 (c-2), e_1 (d-1), e_2 (d-2), f_1 (e-1), f_2 (e-2), h_1 (f-1), h_2 (f-2), h_3 (f-3), ps_1 (g-1), ps_2 (g-2), ps_3 (g-3). Anal region: ad_1 (pa-3), ad_2 (pa-2), ad_3 (pa-1), an_1 (an-1), an_2 (an-2). All genital and "paragenital" setae of Price are homologues of genital setae of other cosmochthonioids.

On the basis of our examination of specimens of *P. lavoipierrei*, we have noted several errors or misinterpretations in Price's descriptions. 1) The palps of pediculochelid mites do not have five "free" segments; the femur and genu are immovably fused, although a partial suture delineates them. 2) The "solenidia" which Price found dorsad of palp and leg insertions are the supracoxal setae (*e* and *eI*, respectively) and not solenidia. 3) *Paralycus lavoipierrei* has five pairs of setae on the ventral subcapitulum, not four (Price missed seta or_1).

4. The three setae of the proximal palp segments of *P. lavoipierrei* are easily
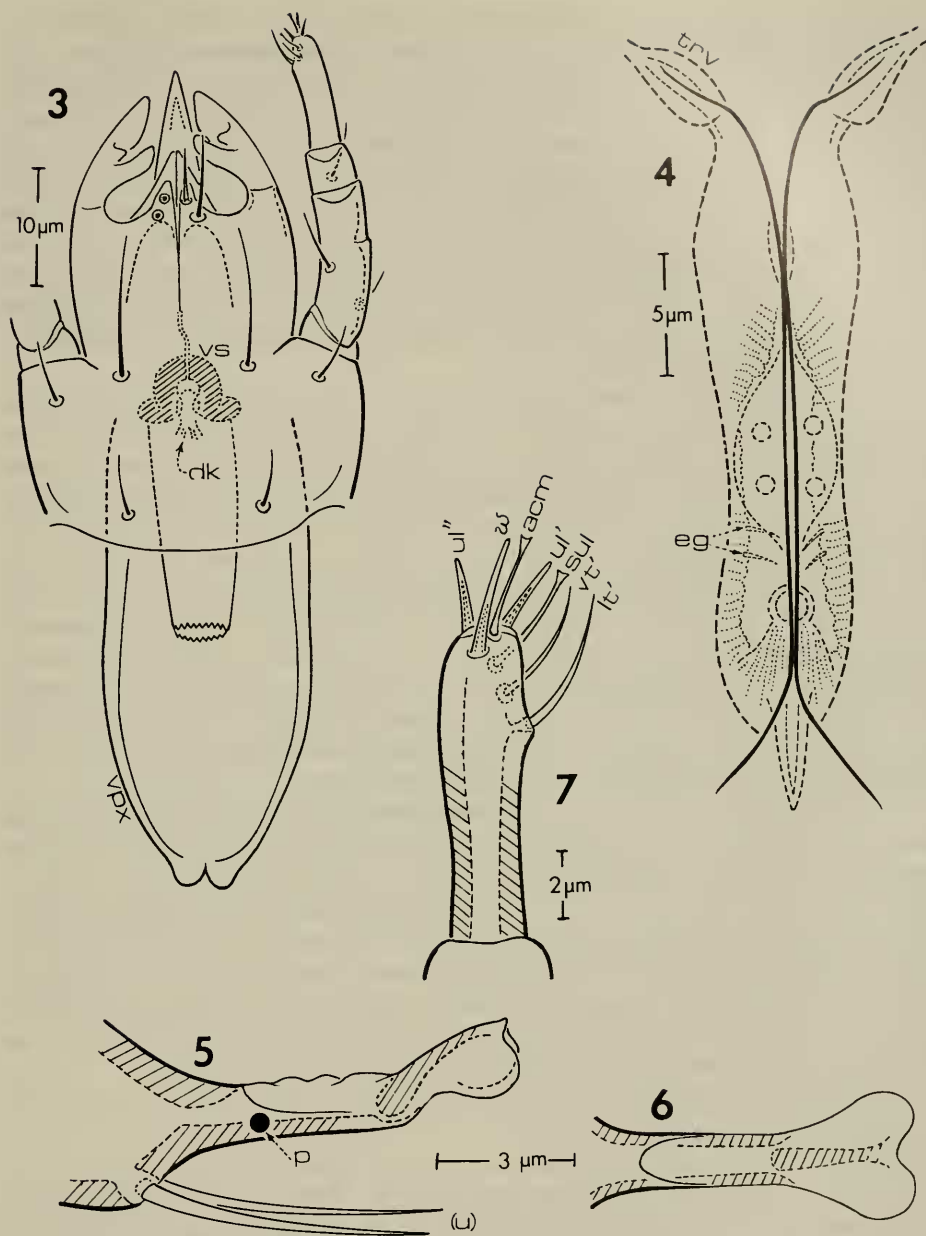
Figs. 3–7. *Paralycus lavoipierrei* adult. 3, Subcapitulum (ventral aspect), removed from body. 4, Genital region. 5, Distal portion of tarsus III (antiaxial aspect). 6, Same, dorsal aspect. 7, Palpal tarsus (dorsal aspect).

homologized with those of other sarcoptiform mites. The two on the femur are *sup* and *inf* (dorsal and ventroparaxial positions, respectively); the dorsal seta of the genu is *ds*. Seta *inf* of other enarthronote mites is formed in the deutonymph, *sup* is larval. The complete ontogeny of *P. lavoipierrei* is unknown, but *inf* is

absent in the larva. *Paralycus parvulus* adults have only *sup* on the palpal femur, a probable neotenic state. Among sarcoptiform mites outside the Astigmata the latter condition, as well as the glabrous genu, is rare (unknown in other Enarthronota); the presence of only *ds* on the tibia (*l'* and *l''* are lost) is apparently unique. Homologies of tarsal setae are less certain, but are postulated in Fig. 7. Next to that of *Fosseremus* (Grandjean, 1965) it is the most regressive sarcoptiform mite palpal setation known to us. Setae *ul'* and *ul''* appear eupathidic, but their canals were not observed. Directly dorsad and ventrad of pair (*ul*) are unpaired setae with expanded tips; these positions are usually occupied by *acm* and *sul,* respectively, and these designations are applied. The single paraxial seta is probably *lt'* and the most proximal ventral seta is positionally comparable to *vt'* of other sarcoptiform mites.

The more proximal dorsal "setiform organ" is most difficult to homologize. There are usually three unpaired dorsal, or nearly dorsal, setiform organs on the palpal tarsus of sarcoptiform mites; the anteroculminal seta (*acm*), which is most distal; the culminal (*cm*), which is usually most proximal; and solenidion ω, which can be exactly dorsal or shifted somewhat antiaxiad. The latter is present as a rule in sarcoptiform mites. The structure in question is hollow, and since *cm* is never eupathidic, nor placed so far anteriad, the latter is apparently lost. Since *acm* is already accounted for, the proximal dorsal setiform organ of this mite is probably solenidion ω; it is so labelled in Fig. 7, but the convention of transversely striating solenidia in illustrations is not followed because of uncertainty. The usual confirmation by examining such organs in polarized light is inconclusive, since none of the normal setae exhibit noticeable birefringence. Only the rutellum and cheliceral digits of *P. lavoipierrei* are clearly birefringent.

5. The leg setation of *Paralycus* is the most regressive of all sarcoptiform mites outside of the Astigmata. Setal formulae (famulus included, solenidia in parentheses) of *P. lavoipierrei* are as follows: leg I, 0-2-4-2(1)-9(1); leg II, 0-2-2-3-6(1); leg III, 1-2-0-2(1)-5; leg IV, 0-2-0-2-5. Shapes and distribution of setae and solenidia are illustrated in Figs. 8–11. The setae remaining in this species are those which are fundamental (larval on I–III, protonymphal on IV) in other sarcoptiform mites. No setae which are typically accessory (added during ontogeny) are present, and many of the usual fundamental setae are themselves lost. Regarding leg setation, neotenic trends are very strong in the Pediculochelidae.

Leg setation of *P. raulti* and *P. parvulus* is similar, except seta *v'* of trochanter III is absent in *P. parvulus.*

As with the palp, setal homologies on proximal leg segments are readily determined; those of some tarsal setae are less obvious. Tarsus IV has only five setae. In contrast, the fundamental setation of tarsus IV in the large majority of sarcoptiform mites comprises seven setae (*ft''*, *p'*, *p''*, *u'*, *u''*, *pv'*, *pv''*). In the few enarthronote genera with five fundamental setae (e.g., *Amnemochthonius, Mesoplophora*), it is the proral pair which is lost, but this is not true of *Paralycus.* The protonymph of *P. lavoipierrei* is undescribed, but from studies of a single larva, and Price's (1973, Fig. 12) illustration of a different larval specimen, there are no setae added to legs I–III during ontogeny, and we assume this is also true of leg IV. It is clearly the primiventral pair (*pv*) which is never formed, a regression otherwise unknown in sarcoptiform mites, and rare in other Acariformes (Grandjean, 1946a).
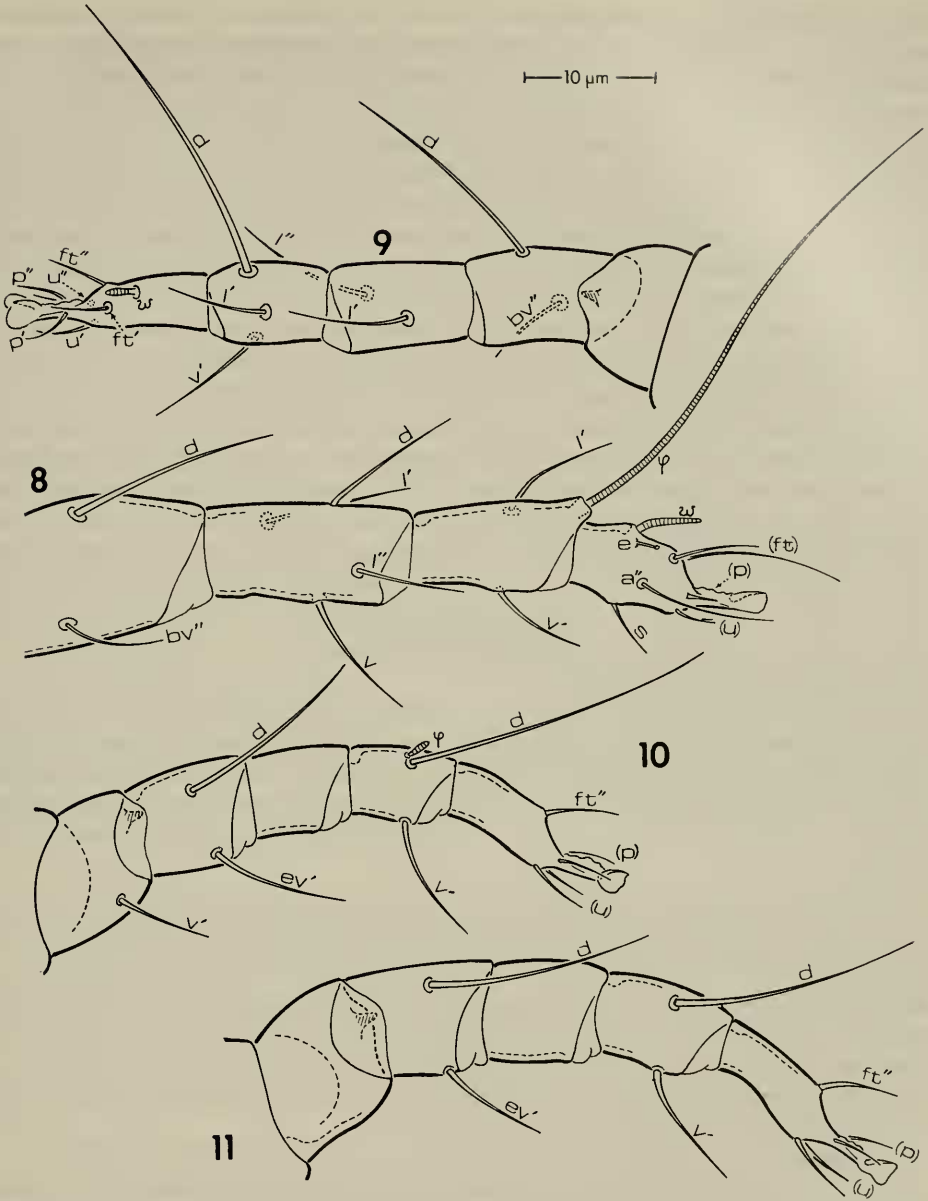
Figs. 8–11. *Paralycus lavoipierrei,* adult. 8, Leg I, trochanter and part of femur omitted (antiaxial aspect). 9, Leg II (dorsoparaxial aspect). 10, Leg III. 11, Leg IV. Figs. 10 and 11 antiaxial aspect, slightly from above.

Tarsus III has an identical setation. In fact, the only setiform organs of leg III not found on IV are trochanteral seta *v'* and tibial solenidion ϕ, which is imperfectly coupled (in separate alveoli) with seta *d*. Tarsus II is similar to that of legs III and IV, except that seta *ft'* is present, as is solenidion ω.

On tarsus I homologies of pairs *(ft)*, *(u)*, *(p)* and the famulus, *e*, are certain. The

prorals appear to be eupathidic, but no canal was observed. The more difficult setae are the remaining more proximal two setae which are in the ventral and antiaxial region. Possible candidates for homologues of the ventral seta are the unpaired subunguinal, *s*, and either of the primiventral pair, *pv'*, *pv''*; because of its exactly midventral position and the regressive tendency of the primiventral pair in the Haplochthoniidae (*pv'* is lost from tarsi I–III of *Amnemochthonius*), we feel the most likely homologue is seta *s*. Candidates for homologues of the antiaxial seta are primilateral seta *pl''* and antelateral seta *a''*. Seta *pl''* has been lost and *a''* is present in both *Haplochthonius* and *Amnemochthonius*; the antiaxial seta of *P. lavoipierrei* is probably *a''*.

6. Seta *d* on each femur, genu and tibia of sarcoptiform mites is a very "strong" seta, in the priority concepts of Grandjean (1946a), unless coupled with a solenidion (genua and tibiae only), in which case it is usually regressive or lost completely, concomitant with hypertrophy of the solenidion, as discussed by Norton (1982). On tibia I of *P. lavoipierrei*, for example, *d* has apparently disappeared; no vestige is visible, such as that found in the Haplochthoniidae. However, on tibiae II and III this post-coupling tendency is not evident. Seta *d* of tibia III is still very large and *ϕ* is short and clavate. More surprisingly, on tibia II solenidion *ϕ* has disappeared, rather than seta *d*. It is clear that *ϕ* was ancestrally present and coupled to *d*, since all other cosmochthonioid mites possess such a state. This is the only instance known to us in which after coupling the solenidion has less priority than the associated seta.

Also surprising is the loss of seta *d* on genu II before the loss of either lateral seta, a state unknown in other sarcoptiform groups except the Astigmata. It might be argued that the seta labelled *l'* in Fig. 9 is simply a seta *d* which has shifted paraxiad, but the alignment with *l'* of tibia II is perfect and if *d* is shifted at all in other sarcoptiform mites, it is to a position slightly antiaxiad of center, not paraxiad.

7. Like their near relatives, the Haplochthoniidae and Cosmochthoniidae, which are common in house and barn debris and periodically dry soils, pediculochelid mites are apparently tolerant of limited environmental moisture. Desiccation tolerance is probably necessary for associations with bees, rats and chickens, such as exhibited by *P. raulti* and the undetermined species reported by Baker and Wharton (1952) and Price (1973). Also, the soils from which members of other species have been collected in California, Italy and Western Australia are subject to long periods of dryness.

It is interesting to compare *Paralycus* with the most dry-adapted of the Palaeosomata, members of the genus *Aphelacarus*. The common species *A. acarinus* (Berlese) has an ecological distribution similar to that of haplochthoniid and cosmochthoniid mites; it is found in periodically or almost constantly dry soils in warm climates and synanthropic situations in some more northerly regions (Grandjean, 1954b). There are several morphological peculiarities which, if not for the weight of previous arguments, might suggest a close relationship between these two taxa. The facies of *Paralycus* is probably closer to that of *Aphelacarus* than any other sarcoptiform mite; it has a similar naso with associated rostral setae, an unsclerotized, elongated body, and even a dorsal division running between setal rows *e* and *f*. Like *Paralycus*, *Aphelacarus* has two pairs of reduced genital papillae and lacks both hysterosomal cupules and tarsal lyrifissures of legs

and palp. *Aphelacarus* possesses an unpaired gland, the long duct of which opens between the bases of the chelicerae. Although undescribed, there is a round, dense "glandular" mass between the cheliceral bases of *P. lavoipierrei*; no duct has been observed. Also surprising is that tibial solenidia of *Aphelacarus* which are closest to setae *d* are in regression and appear almost vestigial. How many of these convergent similarities are associated with adaptation to dry habitats? It seems likely that at least the size and numerical regression of genital papillae can be so categorized. Alberti (1979) has concluded that these papillae function in water absorption in terrestrial acariform mites. Their atrophy or disappearance in *Aphelacarus*, Haplochthoniidae, Cosmochthoniidae, Pediculochelidae, and other groups, such as the Psoroptidia and Hypoderidae (Astigmata), correlates well with preference, or at least tolerance, of environments low in available moisture.

8. The *Paralycus* specimen from Western Australia mentioned above is the first Australian record of the Pediculochelidae. The single adult female examined seemed indistinguishable from Price's California specimens of *P. lavoipierrei*. It is housed in the Field Museum of Natural History, Chicago, and bears the following data: 20 km SW of Exmouth, Goat Cave, Cape Range, 100 meters elev., 29 September, 1976, ex. berlese leaf litter and soil at base of large fig, J. Kethley coll., FMHD #76-352.

Acknowledgments

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Addendum.—While this paper was in press, Dr. D. C. Lee (South Australian Museum, Adelaide) kindly pointed out an oversight. Since Protoplophoridae Ewing, 1917, is an earlier name than Cosmochthoniidae Grandjean, 1947, Article 36 of the current Zoological Code requires the use of Protoplophoroidea instead of Cosmochthonioidea in the sense used by us.